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Elaeocarpus (Elaeocarpaceae) endocarps from the Early to Middle Miocene Yallourn Formation of Eastern Australia

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ABSTRACT
Elaeocarpus cerebriformis sp nov. is described, from near the base of the middle to late Miocene Yallourn Formation of south-eastern Victoria. The ellipsoid, usually trilocular endocarp, and bastionate external ornamentation of the endocarp wall suggest affinities with an undeseribed extant taxon from montane areas of north eastern Queensland.

Introduction

The Elaeocarpaceae is a moderately large, essentially southern hemisphere family with about 520 speeies in nine genera (M. Coode *pers comm.* 1995). Fruit morphology is variable in the family with dehiscent ± woody fruits (*Sloanea, Peripentadenia, Dubouzetia*), berries (*Sericolea, Aristotelia*), and drupes (*Elaeocarpus*, *Aceratium*). The endocarp in *Aceratium* is generally weakly lignified and has prominent and persistent mesocarp fibres, while in *Elaeocarpus* the endocarps are generally woody, strongly ornamented and lack persistent mesocarp fibres. An exception is *E. johnsonii* F.Muell. which has persistent mesocarp fibres, and the endocarp is not woody. The fossil fruits described here are hard, woody, strongly ornamented drupes and therefore are referable to *Elaeocarpus*.

Elaeocarpus has been recognised as a ubiquitous element of the Tertiary floras of eastern Australia, because of the distinctive morphology of the endocarps, and also because the woody endoearps are robust and survive fossilisation (Kirchheimer 1935, Selling 1950, Rozefelds 1990a, Blackburn & Sluiter 1994, Rozefelds & Christophel 1996). The affinities of many of the fossil endocarps that have been compared with, or referred to *Elaeocarpus*, remain poorly studied. The present material was collected from near the base of the Yallourn Formation. It was identified as *Elaeocarpus* by Blackburn (1985), and mentioned by Blackburn & Sluiter (1994, p. 346) who also commented that `pollen types that are comparable with the genus *Elaeocarpus* are common throughout the Yallourn and Morwell coal seams'. Christophel (1994) also illustrated these same specimens but did not examine the systematic placement of this material in more detail. The Yallourn Formation is considered to be Early to Middle Miocene, and is part of the *Triporopollenites bellus* palynological Zone (Blackburn & Sluiter 1994). Holdgate *et al.* (in press) suggest the Yallourn Seam eovers a period of about a million years from 16.5 to 15.5 m. y., at the Early-Middle Miocene boundary (A. P. Kershaw pers comm. 1995).

In this paper, the systematic relationships of this taxon are examined, based upon a comparative study of the endocarps of extant Australian and New Zealand taxa (Rozefelds 1990b, Rozefelds & Christophel in. prep.). A study of endocarps of extant *Elaeocarpus* species from New Zealand and Australia (Rozefelds 1990b, Rozefelds & Christophel in prep.) showed that endocarp morphology is highly variable (Table 2). Similarities in endocarp morphology between the fossil and extant *Elaeocarpus* taxa are recognised and the biogeographical implications of these fossil taxa are discussed.

Materials and methods

The material studied is preserved as 'charcoalified' fruits. Prior to photographing the

TABLE 1. LIST OF EXTANT MATERIAL EXAMINED, INCLUDING LOCALITY, COLLECTOR AND SOURCE OF MATERIAL

Taxon	Locality	Collector
E. arnhemicus F.Muell.	Kennedy River, 15°26'S, 144°11'E SFR 607, Bridle L. A., 16°59'S, 145°36'E	Hyland 11243 (QRS) Gray 2164 (QRS)
E. coorangooloo J.F.Bailey & C.T.White	Mazlin Ck, Tolga-Atherton Road	Hyland 12637 (QRS)
E. grandis F. Muell.	SFR 310, Upper Goldsworthy L. A. 17°14'S, 145°06'E. Noah Creek, Cape Tribulation Area	Gray 2749 (ex QRS) A.C.Rozefelds Coll.
E. ruminatus F.Muell.	SFR 194, Parish of Barron, 17°28'S, 145°28'E.	Gray 3669 (QRS)
E.williamsianus Guymer	near Burringbar, New South Wales	AQ348209 (BRI)
***E.* sp. nov. 1**	SFR 185, Kauri Logging Area, 900m, 17°10'S, 145°35'E	Sanderson 6 (QRS)

TABLE 2. ORNAMENTATION TYPES IN SELECTED EXTANT AND FOSSIL *ELAEOCARPUS* SPECIES, BASED UPON ROZEFELDS AND CHRISTOPHEL (IN PREP.)

Ornamentation Types	Description of Ornamentation in T. S.	Extant Australian species with ornamentation type	Fossil taxon with ornamentation type
Baculate	Rod-like, the maximum diameter of rod is less than height	*E. arnhemicus* F.Muell.	
Bastionate	Width of the bastionate processes is greater than the distance between processes, processes expanded distally	*E. grandis* F.Muell. *E. williamsianus* Guymer *E. sp. nov.*	*E. spackmaniorum* Rozefelds *E. mackayii* (F.Muell.) *E. cerebriformis* Rozefelds & Christophel (herein)
Echinate	Pointed sculptural elements, the largest diameter can be greater or smaller than height	*E. carolinae* Hyland & Coode *E. culminicola* Warb. *E. eumundi* F.M.Bailey *E. ruminatus* F.Muell. *E. reticulatus* Sm.	*E. cunningii* Rozefelds
Granulose	circular to subcircular rounded or grainlike processes	*E. elliffii* Hyland & Coode *E. sericopetalus* F.Muell.	
Punctate	marked with irregularly scattered depressions	*E. bancroftii* F.Muell. & F.M. Bail. *E. linsmithii* Guymer *E. stellaris* L.S.Smith	*E. clarkei* (F.Muell.) *E.* sp. nov. Rozefelds & Christophel, in press
Smooth	uniform relief	*E. thelmae* Hyland & Coode *E. ferruginiflorus* C.T.White *E. foveolatus* F.Muell. *E. largiflorens* C.T.White	
Verrucate	Irregular rounded to globular structures	*E. coorangooloo* J.F.Bailey & C.T.White	

fossil endocarps, the material was whitened with ammonium chloride to highlight surface features and ornamentation. Modern endocarps were photographed without whitening. SEM examination of extant endocarps yielded few additional insights that were not available from examining the material with light microscopy. Comparative extant material of North Queensland *Elaeocarpus* species was provided by CSIRO, Atherton (QRS) and Brisbane (BRI) and the material examined is listed in Table 1. Fossil material is lodged in the Department of Botany, University of Adealide

Results

SYSTEMATICS

Family: Elaeocarpaceae

Elaeocarpus L.

Type species *Elaeocarpus serratus* L.

Elaeocarpus cerebriformis Rozefelds and Christophel *sp. nov.*

Elaeocarpus sp. in Blackburn, 1985, p. 49-50, pl 28, a, b, d. *Elaeocarpus* sp. in Christophel, 1994, fig. 2.10E.

DIAGNOSIS

Distinguished from other *Elaeocarpus* species by the following combination of characters: ellipsoid, 10.1–12.2 mm long, 7.0–8.1 mm wide, three-partite endocarps; bastionate ornamentation, 0.7–0.8 mm high.

DESCRIPTION

Woody endocarp, ellipsoid in lateral view, with three sutures, less frequently two sutures, 10.1-12.2 mm long by 7.0-8.1 mm wide. Apex and base of endocarp rounded in lateral view. Prominent bastionate ornamentation (0.7-0.8 mm high), consisting of irregularly shaped ridges which arise perpendicularly from base of endocarp wall, giving a cerebriform appearance. Wall of endocarp 1.1-1.2 mm thick. Sutures recessed, below ornamentation. Locule in UAY004 is 5.6 mm long by 3.4 mm wide. Seed anatropous, ellipsoid in lateral view, apex broadly rounded.

HOLOTYPE: UAY001. TYPE LOCALITY: Yallourn Formation, Yallourn Coal Mine, Latrobe Valley, Victoria (38°12'S, 146°20'E). (Fig. 1)

ETYMOLOGY

For the cerebriform, brain-like external appearance of the endocarps.

MATERIAL EXAMINED

UAY001-004, Yallourn Formation, Latrobe Valley, Victoria. (Fig. 1)

REMARKS

The endocarp in *Elaeocarpus cerebriformis* (Fig. 2) is ellipsoid in outline, with usually three recessed sutures and bastionate ornamentation. The three sutures indicate that the endocarp was derived from a three locular ovary. In the developed fruit only one locule is evident as the other two have been compressed by growth of the fertile locule. The wall of the seed is preserved but details of the internal structure of the seed are not preserved. Groups of taxa within *Elaeocarpus* can be identified by their endocarp morphology, particularly ornamentation types and endocarp shape (Table 2). The various ornamentation types are given in Table 2. Three extant Australian species have bastionate ornamentation: *E. grandis* F.Muell., *E. williamsianus* Guymer, and an undescribed taxon (*Elaeocarpus* sp. nov. 1, Coode 1984) from north eastern Queensland (Fig. 1; Table 2). The first two taxa have spherical endocarps and hence differ from the ellipsoid endocarps of the fossil material being described here. *Elaeocarpus grandis* also differs from *E. cerebriformis* in that the non-fertile locules are not obscured by growth of the fertile locule (Fig. 4A). The ellipsoid form of the usually trilocular endocarp, and

Fig. 1. Fossil record of fossil *Elaeocarpus cerebriformis* and the modern distribution of extant *Elaeocarpus* sp. nov. is arrowed.

bastionate ornamentation suggest affinities with *Elaeocarpus* sp. nov. 1 from north eastern Queensland. The endocarps of *Elaeocarpus* sp nov. 1 differ from *E. cerebriformis* in being larger c. 14 x 10 mm (Coode 1984), and the ornamentation is also more pronounced i.e. (0.7-1.5 mm high). *Elaeocarpus* sp nov. 1 (*Sanderson 6,* Fig. 3) is restricted to montane heath and rain forest, at Thornton Peak, and the Windsor Tableland, in north-eastern Queensland (Coode 1984).

Coode (1984) was uncertain of the infra-generic placement of *Elaeocarpus* sp. nov. 1, because flowers were not known. He compared it to *E. coorangooloo* using fruit and seed characters. The endocarp of *E. coorangooloo*, like *Elaeocarpus* sp. nov. 1 is ellipsoid in lateral view. It differs from *E. cerebriformis*, in the more rounded, verrucate ornamentation of the endocarps, and usually bilocular endocarp. *Elaeocarpus arnhemicus* is also comparable to *E. cerebriformis* in that it has ellipsoid endocarps, with prominent processes. It also differs from *E. cerebriformis* in having a bilocular endocarp, and the processes are baculate in form.

Coode (1984) emphasised the importance of seed characters, in defining groups within *Elaeocarpus,* particularly whether the embryo was curved or straight. The wall of the seed is preserved in *E. cerebriformis* but it is not possible to determine whether the embryo was curved or straight (Fig. 4A). *Elaeocarpus arnhemicus*, *E. coorangooloo* and *E.* sp. nov. 1 all have straight embryos. It would seem likely therefore that *E. cerebriformis* also had a straight embryo. The alternative possibility is that the trilocular condition in *E. cerebriformis* implies affinities to the *E. foveolatus* group or *E. ruminatus*, although the ornamentation in these taxa differs in being smooth or echinate (Table 2, Figs. 4B & 4C).

Two fossil taxa, *E. mackayii* (F.Muell.) Kirchheimer and *E. spackmaniorum* Rozefelds, have bastionate ornamentation and could be compared to *E. cerebriformis* (Table 2). These taxa both differ from *E. cerebriformis* in being spherical in shape. *Elaeocarpus spackmaniorum* also differs from *E. cerebriformis* in that the non-fertile locules are not obscured by the development of the fertile locule.

Discussion

Elaeocarpaceae pollen of uncertain affinities were recorded from the Latrobe Valley Coal Measures (Luly *et al.*, 1980, Sluiter & Kershaw 1982). Blackburn & Sluiter (1994)

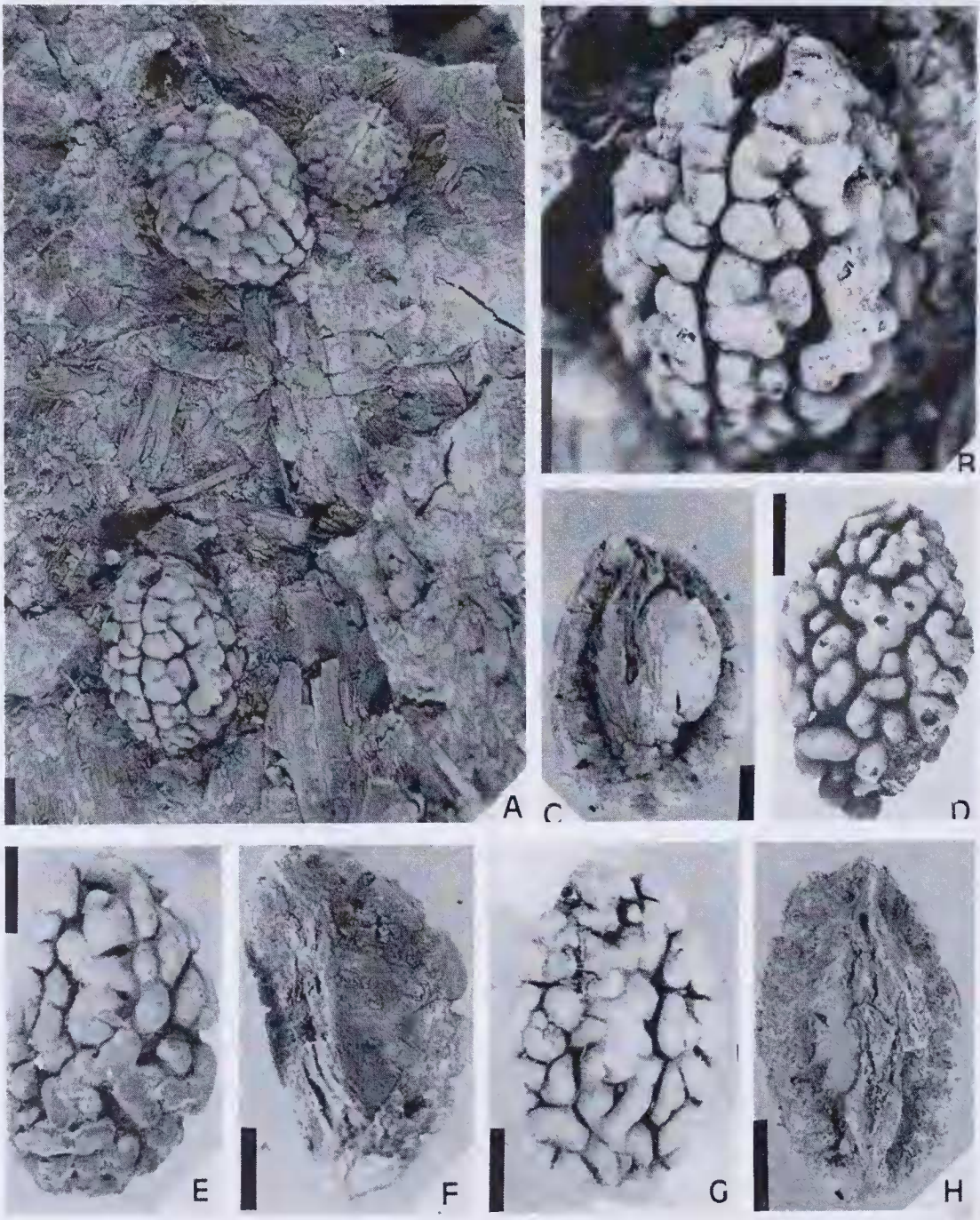

Fig. 2. *Elaeocarpus cerebriformis* from Yallourn Formation, Yallourn Coal Mine, Victoria. a - Holotype (UAY001) and paratype (UAY002) in matrix, Holotype lower specimen. b - Holotype enlarged to show details of prominent bastionate ornamentation. c - Internal view of part of endocarp (UAY004) showing anatropous seed in place. d - External view of part of endocarp (UAY003) showing bastionate ornamentation. e-h - External and internal views of parts of the endocarps of paratype (UAY004), illustrating the variation in ornamentation within one endocarp. Scale bars = 0.25 cm.

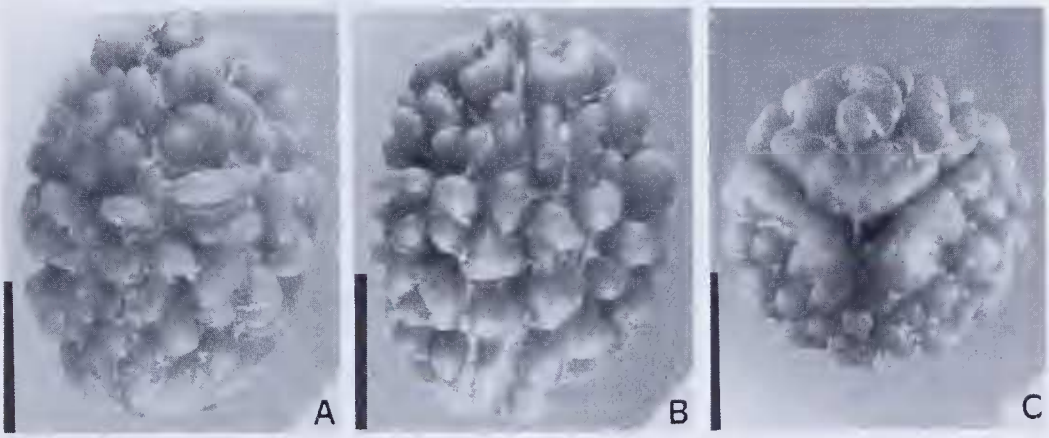

Fig. 3. *Elaeocarpus* sp. nov. 1 (Sanderson 6). a - Mesosutural view. b - Sutural View. b - Apical view. Scale bars = 0.5 cm.

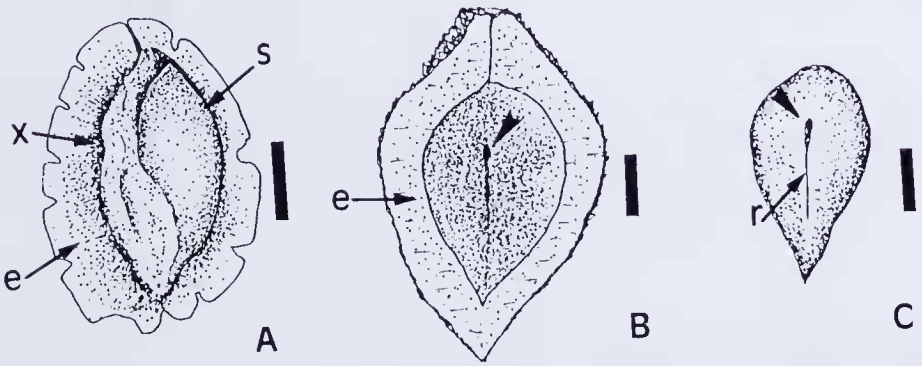

Fig. 4.**a** - *Elaeocarpus cerebriformis*. Drawing of part of endocarp of UAY004, showing seed in place in locule, and an adjacent compressed locule. **b** - Longitudinal section through endocarp of *E. ruminatus* with seed removed showing the attachment scar. **c** - Seed of *E. ruminatus* showing attachment scar (arrowed) and raphe. (e, endocarp; x, compressed locule; s, seed; r, raphe). Scale bars = 0.25 cm.

considered that some of Elaeocarpaceae pollen types were comparable with *Elaeocarpus*. The fossil endocarps, and probably the pollen, indicate that *Elaeocarpus* was a ubiquitous element of the Yallourn palaeoflora.

Elaeocarpus in Australia is essentially a rain forest genus restricted to mesic forest communities. This fruit record would support the existing palynological literature that rain forest communities were present in the Early to Middle Miocene in the Yallourn area (Sluiter & Kershaw 1982). Interseam clays at the base of the Yallourn Formation have also yielded fruits i.e. Menispermaceae, Vitaceae and Proteaceae with rain forest affinities (Rozefelds 1995).

A diverse range of ornamentation types occurs in the endocarps of extant *Elaeocarpus* species in Australia (Table 2). Most of these ornamentation types are represented by taxa in north eastern Queensland, which is the centre of diversity for the genus in Australia. Fossil taxa with a range of ornamentation types have also been recognised in mid Tertiary deposits in eastern Australia. The new fossil taxon *E. cerebriformis*, and previously described *E. spackmaniorum* Rozefelds and *E. mackayii* (F.Muell.) Kirchheimer, have bastionate ornamentation. *Elaeocarpus cunningii* Rozefelds has echinate ornamentation, and Rozefelds & Christophel (1996) are describing taxa with punctate ornamentation (Table 2). The extensive fossil record of *Elaeocarpus* in Australia, as exemplified by the diversity of fruit morphotypes in the mid-Tertiary, indicates that the genus was morphologically diverse at this time. The fossil record of *Elaeocarpus* in southern and eastern Australia also suggests that montane and lowland rain forests near Cairns, in north eastern Queensland, are a refugia for taxa with affinities to these mid-Tertiary species.

A number of endemic *Elaeocarpus* species in north eastern Queensland (e.g. *E. sp. nov.*, *E. linsmithii*, *E. thelmae*, *E. johnsonii*) are restricted to montane habitats. Endemism is common in montane floras in tropical and subtropical regions e.g. Hawaii and Afro-alpine floras of eastern African mountains (Stott 1981, Cox & Moore 1980). A high level of endemicity also occurs in *Elaeocarpus* in New Guinea and New Caledonia and this is probably related to the physiographic and edaphic variation of these islands (Coode 1978, Tirel 1982). Stott (1981) presented two hypotheses to explain the origin of mountain endemics; i.e. that the isolated conditions in montane floras, prevents inflow of potential competitors and evolution is accelerated, and the relictual populations differentiate through adaptive radiation and vicariance. Alternatively, Stott (1981) proposed that these relictual floras have been stranded on mountain tops through climatic change.

The most closely related taxon to *Elaeocarpus cerebriformis* occurs in montane rain forests in north eastern Queensland. The Yallourn Formation was a low altitude depositional environment, and the presence of the closest analogue in high altitude montane forests suggests possible altitudinal change, and reduction in range, and/or migration since the mid-Miocene. Reduction in range and/or migration of taxa, and altitudinal displacement, can be correlated generally with the increasing aridity of the climate from the Miocene onwards (Sluiter & Kershaw 1982).

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